

Faithful replication of foraging techniques along cultural transmission chains by chimpanzees and children

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Observational studies of wild chimpanzees (*Pan troglodytes*) have revealed population-specific differences in behavior, thought to represent cultural variation. Field studies have also reported behaviors indicative of cultural learning, such as close observation of adult skills by infants, and the use of similar foraging techniques within a population over many generations. Although experimental studies have shown that chimpanzees are able to learn complex behaviors by observation, it is unclear how closely these studies simulate the learning environment found in the wild. In the present study we have used a diffusion chain paradigm, whereby a behavior is passed from one individual to the next in a linear sequence in an attempt to simulate intergenerational transmission of a foraging skill. Using a powerful three-group, two-action methodology, we found that alternative methods used to obtain food from a foraging device ("lift door" versus "slide door") were accurately transmitted along two chains of six and five chimpanzees, respectively, such that the last chimpanzee in the chain used the same method as the original trained model. The fidelity of transmission within each chain is remarkable given that several individuals in the no-model control group were able to discover either method by individual exploration. A comparative study with human children revealed similar results. This study is the first to experimentally demonstrate the linear transmission of alternative foraging techniques by non-human primates. Our results show that chimpanzees have a capacity to sustain local traditions across multiple simulated generations.

culture | diffusion chain | social learning | tradition

Long-term observational studies of wild chimpanzees (*Pan troglodytes*) across Africa have revealed a diverse range of behavioral differences between populations, thought to represent local traditions (1–3). The inference that the differences are socially learned is based on (i) patterns of distribution that appear incompatible with genetic or simple environmental explanations; (ii) records of close observation of adults by infants as well as matching of mother–offspring foraging styles (4–7); and (iii) studies of both wild (8–10) and captive chimpanzees (11–15) showing that social learning from conspecifics can affect the acquisition of tool-use skills. Each wild chimpanzee community exhibits a distinct profile defined by several different kinds of putative traditions that have been described as cultures. In recent years, complexities of these kinds have increasingly been reported in other wild primates [orangutans (16), capuchins (17, 18), and taxa such as cetaceans (19)].

However, the evidence from the wild is essentially circumstantial and correlational. Although some researchers have gone to great lengths to establish that the presence of a behavior pattern at one site but not another is not dictated by the availability of raw materials (20, 21), skeptics have emphasized that it is not possible to identify all relevant factors (22–24). Some behaviors of wild chimpanzees, such as termite fishing, have now been recorded over multiple generations (7) (E. Lonsdorf, personal communication). Yet, whether such behav-

iors are culturally transmitted requires evidence that chimpanzees can transmit behavior with sufficient fidelity for distinct behavioral variants to be maintained.

Controlled experiments would, in principle, be able to provide this evidence, but field experiments face obstacles that have yet to be surmounted. Matsuzawa and colleagues (8, 10, 25, 26) have pioneered an "outdoor laboratory" to document the transmission of nut-cracking behavior in the wild, but the logistics of such studies have limited the application of control conditions possible in captive experiments, in which some chimpanzees see no model, allowing a more conclusive establishment of the role of social learning.

About 30 controlled social learning experiments (27, 28) have been conducted with chimpanzees. The relevance of this work to the traditions of wild chimpanzees is limited, however. First, of the 22 studies tabulated in the most recent review (28), 14 used human models, not chimpanzee models, and it is unclear that such models are as effective as conspecifics. Second, 17 studies were restricted to dyadic learning between a model and an observer. However, what we really need to establish is whether chimpanzees learn from each other with sufficient fidelity for behavior to spread within a community. Thus far, only four experiments concern the spread of behavior at the group level (11, 15, 29, 30). None of these investigations used a no-model control group, however, which might have demonstrated that the spread of behavior was not due to a gradual rise in individual learning.

To remedy these limitations, we recently conducted an experiment with a powerful "three-group, two-action" design (31). One chimpanzee from each of two social groups was trained to solve a foraging task using one of two alternative techniques. Members of each group were then allowed to observe the trained model, resulting in the differential spread of each foraging technique within the two different groups. Members of a third control group who did not observe a model failed to solve the task. This finding is therefore of direct relevance to the question of culture in wild chimpanzees.

However, one significant limitation in our study can only be overcome by the complementary approach of the present experiment. Because the whole group had access to the device throughout the previous study, it was not possible to track precisely who learned from whom. At one extreme, all may have learned by watching the initial model; alternatively, each may have learned something from all, many, or just one of those who mastered the task before them. In the present study, we instead employ a "diffusion chain" paradigm that allows accurate tracking of exactly who learns from whom over a number of transmission events. Just one individual was allowed to watch the

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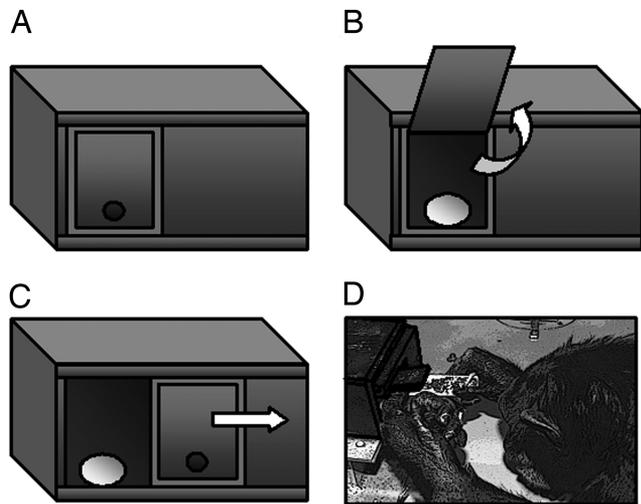


Fig. 1. Dorian Fruit apparatus. (A) The starting position with door closed. (B) Lift method. (C) Slide method. (D) Outlined photograph of model GG performing lift method.

initial model, and then was allowed a solo attempt; once successful, they became the model for a third individual, with the original model excluded, and so on along a chain of transitions that simulate “cultural generations” for the behavior.

Diffusion chains were originally used by Bartlett (32) to study how narrative stories changed as they were transmitted between successive pairs of people, forming a chain. The essential idea was later used in other human studies (33) and in a small number of animal experiments addressing the transmission of predator avoidance in birds (34, 35), food preferences and foraging in rats (36–38), and foraging pathways in fish (39). This literature fails to cite what was arguably the first animal diffusion study (40), in which habituation to novel play objects was transmitted among 19 young chimpanzees. With the exception of ref. 38, diffusion studies have typically compared only one chain with the actions of a control group. It is therefore difficult to determine whether the transmission of behavior involved learning a new action or learning only that a desirable result could be attained by using an action the subjects were already predisposed to. By contrast, in the present study, we return to our three-group, two-action design, in which each of two diffusion chains begins with a model trained to tackle a foraging problem in a different way, while a third, control group sees no model. Any differential transmission in the chains then implies that the specific techniques have been maintained by social learning. The study was conducted with three groups of chimpanzees from Yerkes National Primate Research Center’s Field Station: FS1 (chain 1), FS2 (chain 2), and FS3 (no-model control group). Each of the two chains was initiated by a model trained to either lift a door (FS1) or slide a door (FS2) to retrieve food from a foraging device (named the “Dorian fruit” after the door mechanism as a play on the durian fruit, a popular orangutan food; see Fig. 1A). In the lift door method, the door frame remained in place while the door was lifted up (Fig. 1B and D). In the slide door method, the door remained closed while the frame slid to the right (Fig. 1C; and see Movies 1 and 2, which are published as supporting information on the PNAS web site).

In each chain, a naïve observer was allowed to watch the model retrieve food from the Dorian fruit. Once the observer had seen ≈ 10 successes, they were given an opportunity to interact with the Dorian fruit alone. Observers who successfully opened the Dorian fruit 10 times then became the model for the next chimpanzee in the chain. This methodology generated a chain of six chimpanzees from FS1 group who exclusively used the lift

door method and a chain of five chimpanzees from FS2 group who used the slide door method. Chimpanzees were excluded from the chains and hence became “side branches” if they failed to observe at least one demonstration by the model or were unable to consistently succeed and therefore could not reliably act as a model for the next individual. Six control chimpanzees from FS3 group interacted with the Dorian fruit without observing a model. Three failed to open the door, two used the lift door method, and one used the slide door method. Building on the pioneering work of Menzel *et al.* (40), our study uses diffusion chains to systematically examine whether a non-human primate species is able to accurately transmit a foraging behavior across multiple simulated “cultural generations.”

Human culture provides an inevitable benchmark against which to evaluate animal studies. For an explicit comparison, we replicated our chimpanzee study as closely as possible with human children, focusing on 3-year-olds, following earlier research indicating that this age group represents a sensible cognitive comparison with chimpanzees (41–43). Moreover, it is well known that children of this age group readily learn from the cultural phenomena that surround them (43).

Results

Chimpanzee Study. Behavior of the model. We found that chimpanzees typically opened the door multiple times before retrieving a reward. Because the slide door method was spring-loaded, it often took several attempts to catch and keep open the door. When attempting to lift the door, chimpanzees often had to flick it up several times before it could be held open. Each such lift/slide was scored, because observers could potentially gain useful information every time the door was opened. We determined that observers must witness 10 reward retrievals before being allowed to interact with the Dorian fruit alone. However, it was possible to witness many more door openings. The number of door openings was not used as a criterion for sufficient observation because some models performed 10 or more door openings before retrieving the first reward.

Observation of the model. In practice, observers sometimes displaced the model from the apparatus before they had witnessed 10 complete demonstrations. However, all chimpanzees who met the criteria for inclusion in the main chains witnessed at least one demonstration of door opening during their observation phase (median number of observations FS1 = 5, range 1–24; median FS2 = 8, range 1–17; see Table 1, which is published as supporting information on the PNAS web site). There was no significant difference between FS1 and FS2 in the number of demonstrations that were observed.

In both chains, two forms of co-action were observed between the models and observers: (i) door co-action (of lift or slide) occurred when the observer touched the door or the hand of the model while he/she opened the door; (ii) retrieval co-action occurred when the observer touched the hand of the model as he/she used their fingers to retrieve rewards from the opened Dorian fruit. In FS1, door co-action occurred once between RI and TA and once between MA and MS (both mother–daughter pairs). Retrieval co-action occurred once between TA and MA (unrelated) and twice between MA and MS (mother–daughter). In FS2, door co-action occurred once between ER and AM, once between ER and CY, and twice between BB and KE, and retrieval co-action occurred twice between CY and VV (all unrelated pairs). Even more remarkable, on two occasions, model ER slid the door and held it open while VV (unrelated) inserted her fingers to retrieve rewards.

Transmission of modeled behavior. In FS1, model GG initiated the chain using the lift door technique, which was passed between a further five individuals in the diffusion chain, thus demonstrating five transmission events. During the observation phase, observers watched a mean of 65% of the model’s lifting actions (range

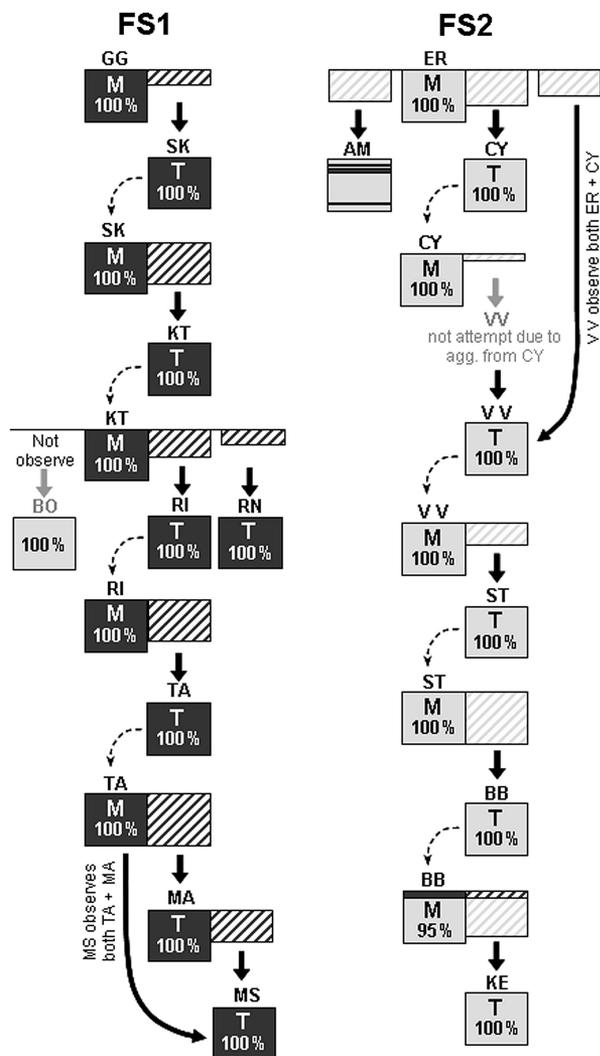


Fig. 2. Diffusion chains starting with a model performing either the lift (*Left*) or slide (*Right*) method. The ID code of each chimpanzee is in bold (GG is the initial model performing lift; ER is the initial model performing slide). Dark shaded areas represent the percentage of door opening that involved lift, first when tested solo (T) and later when in the role of model (M) for the next, naïve, chimpanzee in the chain. Dark hatched areas represent the percentage of a model's lift actions watched by the naïve chimpanzee, and light hatched areas represent the same for slide actions. Dashed arrows indicate each individual's progression from the "T" (test) phase to the "M" (model) phase. Filled arrows mark pairings of each competent model with the naïve chimpanzee that followed them in the chain. Individuals excluded from chains were BO (did not observe the model), RN (failed model motivation check), AM (was not efficient at the task and withdrew), and CY (was aggressive toward the observer).

25–100%). Except in the single instance when BO displaced model KT (see below), all chimpanzees in this chain performed the lift method exclusively both in their test phase and when acting as a model (Fig. 2), which was accordingly transmitted with 100% fidelity from GG, along the chain, to the sixth and final generation. At the end of the chain, MA would not participate without her daughter MS. Hence, when MS's turn came, she had observed both TA and MA before going on to a successful performance, and therefore her acquisition of the lift door technique cannot be considered as consecutive linear transmission from MA.

In FS2, model ER initiated the chain using the slide door technique, which was passed along a diffusion chain of five

individuals. Observers watched a mean of 54% of the model's slide actions (range 3–100%). They exclusively performed the slide method, with the exception of BB, who performed one lift action when acting as a model for KE. KE observed this lift action as well as 78% of BB's much greater number of slide actions, then went on to perform slide actions exclusively herself (Fig. 2). Accordingly, the slide method was transmitted along this chain with 100% fidelity by the fifth and final generation.

Two chimpanzees in each group failed to meet the criteria for inclusion in the chains and therefore became side branches to the linear chains (Fig. 2). In FS1, BO did not observe the model she was paired with (KT), whom she was able to displace, and so attempted the task independently. She discovered the alternative method (slide) to that active in the existing chain (lift). Having failed to observe a single demonstration, she did not meet the criteria for subsequent inclusion as a model (note that a chimpanzee discovering the alternative method after watching the model *would* meet the criteria for becoming the next model). Second, RN acted successfully during her test phase after watching model KT but failed her premodel motivation check on two consecutive days, becoming a side branch. In FS2, AM, who was initially successful, had such limited dexterity to extract rewards that he became frustrated and unwilling to participate and so became a side branch to the FS2 chain. Then, model CY was aggressive toward observer VV, and although VV observed one demonstration, she was subsequently reluctant to approach the apparatus. Because VV's reluctance to participate was due to social incompatibility with CY, she was paired with model ER and went on to succeed.

It might be objected that this methodology would exclude possible corruption of the behavior that may occur in the wild. However, our experiment was designed as a simulation of intergenerational transmission, where in the wild a youngster will typically have seen its elders perform extractive foraging techniques many times before making a successful attempt itself. Hence, we made observation of at least one demonstration a condition of inclusion.

Excluding the side branches, transmission data concern the performance of six participants in FS1 and five in FS2, all of whom performed like the respective models in their group, resulting in a significant difference in the performance of each method (lift:slide ratio in FS1 of 6:0 versus 0:5 in FS2, Fisher's exact test, $P = 0.002$). Four "blind coders," unfamiliar with the identities of the chimpanzees, were able to determine with 100% accuracy whether they belonged to the lift or slide chain, after watching a short section of video from each chimpanzee's test phase. If side branches are included in the analysis to test the overall social learning effect (RN and MS in FS1, CY and AM in FS2; see Fig. 2), the contrast is even more robust (Fisher's exact test, $P = 0.001$).

The original models from each group (ER and GG) were both trained to use the tool to retrieve rewards. However, this was an added level of complexity that was not necessary, because participants (with the exception of AM) could usually reach the rewards with their fingers. The tool was used by all participants in FS1 with the exception of RI and MA. In FS2, the tool was used by only ER and CY. We do not believe that this contrast between FS1 and FS2 necessarily indicates social diffusion of tool use in FS1 because tool use seemed to be more helpful in extracting food by the lift method. For this reason, and because tool use was not the focus of the study, we do not discuss these results further.

No-model control group. The six chimpanzees from FS3 who participated as controls were highly motivated to retrieve the reward, giving food grunts as they observed the apparatus being baited. Three of the six controls successfully opened the door, with two discovering the lift method and one discovering the slide method. The unsuccessful controls spent much of the

successful, the apparatus was rebaited for a total of 10 reward retrievals.

Child Study. Procedure. As with the chimpanzees, at the start of each chain, a child was trained to exclusively use one opening method: slide or lift. The second child in the chain was then brought into the room and asked to wait while the first child performed two demonstrations; then it would be his/her turn. No explicit instructions were given about watching or teaching. After the model's demonstrations, the observer had two solo attempts and if successful became the model for the next child, and so on down the chain. Unlike the chimpanzee study, each step in the child diffusion chain was conducted on the same day.

No-model control group. Children were introduced to the Doorian by the experimenter (EF), who said, "lots of boys and girls have had a turn playing with this box, now it's your go." If the child was unsuccessful after 2 min of interaction with the apparatus, the experimenter offered an explicit hint: "look at the front of the box, at the door, what do you think you do?" Children were allowed to interact with the Doorian until they were successful, which was defined as opening the door fully (either by lifting or sliding), until they refused to participate after a further prompt ("look at the front of the box, at the door, what do you think you do?"), or after 4 min and 30 sec without success. Data were later analyzed for responses both before and after a hint was given.

Analysis. Videotapes were scored to determine the number of "lift door" and "slide door" actions used by each participant in their role as both observer and model. For the chimpanzee study, tapes were scored by two experimenters, and any discrepancies in scores were reconciled by reviewing the videotapes. In addition, four coders unfamiliar with the identities of each participant or the hypotheses of the study were asked to estimate whether each chimpanzee came from a lift or slide chain. For both chimpanzees and children, the tendency to use one method over the other was compared by using Fisher's exact test. All statistics are two-tailed.

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